THE AQUATIC ADAPTATIONS OF PYRAUSTA PENITALIS GRT. (LEPIDOPTERA).*

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INTRODUCTION.

The unique and ingenious methods whereby aquatic animals have solved their problems of maintenance are always interesting, particularly in a group having an immediate terrestrial ancestry, as is the case with aquatic insects. It is a well-known fact that among insects all graduations between the terrestrial and aquatic species can be found, often within one family. Similar transitions are now known to exist within a single species. Some of these transitional forms, while retaining certain terrestrial habits and potentialities, have progressed far in the development of aquatic adaptations and solve the problems of the new environment with remarkable ease. While Lepidoptera are preëminently terrestrial, there exists a very small, heterogeneous group of species which presents aquatic adaptations of peculiar interest. The climax in aquatic adjustment for this group is probably represented by the gilled caterpillars of *Nymphula* (Welch, 1916). *Pyrausta penitalis* Grt., on which this paper is based, presents a striking case, not only of transition from terrestrial to aquatic habit, but also of a development of physiological adaptations which parallel closely those appearing in certain other unrelated Lepidoptera (Welch, 1914).

The field data used in this paper were secured during the summer of 1917, while the writer was a member of the Ohio State University Lake Laboratory staff. In the protected coves of Sandusky Bay, Lake Erie, particularly Beimiller's Cove, *Nelumbo lutea* grows abundantly and during July, 1917, there appeared upon this plant large numbers of the caterpillars and pupæ of *Pyrusta penitalis*. The abundance of material and the constant presence of practically all degrees of development made possible a wide range of observations in a relatively short time. Since the writer has spent but the one season at

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the Lake Laboratory, this report is incomplete in many respects, but the data contained herein are presented with the hope that they may serve as an added basis for future work.

Several papers already published contain information on this insect, but in all of them the data are meager and fragmentary, the sum total representing a very incomplete account. Smith (1890a; 1890b) discussed it under the name *Botis nelumbialis*, giving account of the imago, mature larva, and pupa. Later, Hart (1895) described in more detail the stages of the life-history and presented a few biological features of the larva and pupa. Recently, Chittenden (1918) recorded some interesting terrestrial activities of this species.

Coquillett (1880) described what he thought to be the larva of "Botis penitalis," stating that it fed on Indian hemp (*Apocynum cannabinum*). Chittenden (1918, p. 454), however, points out a certain disagreement of Coquillett's description with the true larva of *penitalis* and suggests the probability that some other species was under observation. Dr. J. McDunnough, in a recent letter to the writer, confirms the suspected error in this record and states that the *Apocynum* feeder is the allied *futilalis* Led. and that he has bred the latter in abundance at Decatur, Illinois.

The writer wishes to express his indebtedness to Dr. J. McDunnough for confirmation of the identification of this species.

THE LIFE-CYCLE.

In the above-mentioned papers are found accounts of the full-grown larva, the pupa, and the imago and further mention is not required here. However, the eggs and place of oviposition have heretofore remained undescribed. The writer, after much searching, finally found, on July 28, a single egg-mass on the upper side of a *Nelumbo* leaf, which, when brought into the laboratory and kept in an aquarium yielded larvæ that were unquestionably those of *penitalis*. This mass was amber-colored, and approximately circular in contour, having a diameter of 3 mm. About sixty eggs were present, surrounded by an amber-colored matrix, and closely set together. On hatching, the egg-shells lost the amber color and assumed a dirty grey appearance. All of the eggs developed normally and larvæ emerged, but since the exact time of the oviposition of the mass was unknown, the length of the egg-stage could not be determined. The young larvæ, at the time of hatching, were about 1.5 mm. long. They immediately began feeding upon the leaf in the vicinity of the egg-mass, consuming the upper surface in the characteristic manner. The surface webbing, described later, appeared very soon, subsequent development and activities continuing in the fashion normal for the species.

The difficulty of finding the egg-masses is quite puzzling since the writer examined hundreds of *Nelumbo* leaves and the amber color of the egg-mass against the green background of the leaf, if that be the usual place of oviposition, should make detection rather easy. Furthermore, the writer observed dozens of leaves each bearing very small larvæ which, it would seem, must have emerged from eggs deposited very near by, but no indications of old egg-masses were detected.

Chittenden found a considerable number of these larvæ boring into the canes of raspberries and likewise, to some extent, in the stalks of corn. However, he states (p. 455), that "there is no evidence that the species feeds on either healthy corn or raspberry, although it feeds on the pith to a considerable extent, but on the contrary develops chiefly upon lotus and other aquatic or semiaquatic plants and enters cornstalks and the cut ends of raspberry canes chiefly as a retreat for passing the winter and for subsequent transformation." This statement is not entirely clear. It seems to imply that corn and raspberry may not be affected unless in some unhealthy condition. It also appears to suggest that these larvæ pass their early development in aquatic situations and then some of them migrate to certain terrestrial plants in order to find a hibernation place. Chittenden has tried to formulate "an approximate life history" from the fragmentary bits of available information and suggested that the larvæ constitute the hibernation stage; that the adults begin emerging in March; that larvæ appear in due course of time and feed until late in August when they complete their growth, seek a convenient winter retreat and hibernate. Such a statement suggests only one generation per year.

Certain observations of the writer do not seem to corroborate the above-mentioned inferences. It was not possible to determine the hibernation stage and it may be that some of the larvæ, in late autumn, do migrate to shore and find hibernation quarters in connection with other plants. However, *Nelumbo* often occurs somewhat remote from shore and while, as will be shown later, these larvæ are efficient swimmers, it seems rather doubtful if such is the only method. Since pupæ are found in the upper end of the *Nelumbo* petioles during the summer, the writer is inclined to suspect that hibernation, in the aquatic situations, may occur as pupæ in cocoons within the old food plants. Circumstantial evidence also seems to indicate more than one generation per year. During the first week in July, larvæ of all sizes as well as pupæ were found and from that time to early August, when the writer's observations ceased, adults were emerging continually from the *Nelumbo* petioles. Quite a number of such pupæ were reared in aquaria in the laboratory. Since these immature forms occurred in connection with the fresh leaves and petioles and were of all sizes and ages, the evidence seems clear that they were not overwintering individuals. Furthermore, the emergence of adults throughout the most of July (and possibly to some extent later) and the finding of eggs on July 28th, suggests a midsummer brood. Therefore, the writer is inclined to believe that in the region of Lake Erie the species is at least double-brooded and that hibernation may occur in connection with the aquatic food-plants.

ADAPTATIONS TO AQUATIC SURROUNDINGS.

The chief aquatic adaptations manifested in this species are related to the problems of food-getting, locomotion, and respiration—problems which are always of vital importance in the adjustment of an animal of terrestrial origin and organization to partial or complete aquatic life. While this species thrives under the conditions of its aquatic surroundings, it is interesting to note that the complete, original terrestrial organization has apparently been retained, that no structural features of aquatic importance have appeared, and that the adjustments to the water are very largely, if not entirely, physiological, consisting of habits and activities which result in the favorable solution of the problems involved. The physiological adjustments of this species to water offer a very close and interesting parallel to those of *Bellura melanopyga* Grote (Welch, 1914) a species which is remote from *Pyrausta penitalis* in kinship, but which has solved its major problems of locomotion, nutrition, protection, and respiration not by structural developments, but by modified activities remarkably similar to those of *P. penitalis.*

FEEDING HABITS.

Food Plants.—In the Sandusky Bay region, *P. penitalis* was found only on *Nelumbo lutea.* Other plants in the same habitats and on nearby shores were examined from time to time, but appeared to be unaffected by this insect. However, it is evidently a general feeder, since other writers have reported it on *Polygonum incarnatum*, *Polygonum hydropiperoides*, *Eupatorium* (species not given), and *Nelumbo nucifera* ("Egyptian lotus"). An erroneous record of *Apocynum cannibinum* was mentioned on a foregoing page.

Leaf-feeding Period.—Two well-defined periods can be recognized in the feeding activities of the larvæ, (1) an early one, the *leaf-feeding period*, and (2) a later period, the *petiole period.* These two periods were given bare mention by Smith (1890a) and Hart (1896, pp. 180-181), but the details and adaptations have not been described.

After hatching, the young larvæ feed upon the outer surface of the *Nelumbo* leaf, removing the upper epidermis and a considerable part of the underlying chlorophyll-bearing tissue. The feeding areas are irregular and vary in size, depending upon the amount of feeding done. They often become confluent, forming large irregular areas. When first made, they are light greenish, but soon change to brown and in time the whole leaf, if heavily infested, assumes that color.

While any part of the upper leaf surface is subject to attack, feeding at the periphery differs, in certain distinct respects, from that within the periphery, and likewise involves distinct differences in accompanying adaptations. These activities will be described in the reverse order of mention.

Leaves bearing young larvæ almost invariably show, when examined critically, numerous, very fine strands of silk all over the upper surface, marking the routes of the wandering larvæ. This apparent wastefulness in silk production is perhaps the first form of aquatic adaptation to appear in the life-cycle since the silken thread continually anchors the tiny larva to the leaf during its search for an appropriate feeding place and aids in preventing it being washed off the leaf by waves or other surface disturbances. When active feeding begins, the silk formation becomes a more noticeable and important feature. Feeding areas are surface excavations, usually with a depth greater than the diameter of the caterpillar, across which is spun a fine, somewhat substantial silk web, and under which the larva works and rests. Frequently, the threads are tied across from one radiating leaf vein to the adjacent one with sufficient tension to pull them slightly towards each other, thus producing a depression beneath the web and providing a retreat for the larva. These nets are of varying extent, but since they are a constant accompanying feature of surface feeding, an attempt was made to determine their significance. That they play some real part in the life of the larvæ is manifested by the fact that while individuals occasionally leave the web-covered tunnels for a certain amount of wandering, they almost invariably return to the original ones or preëmpt others which happen to be empty. Since the leaves of *Nelumbo* rest upon the surface of the water, wave-action, even of a slight degree, often inundates them and, unless protected in some way, the young caterpillars would be constantly exposed to the serious menace of being washed off. A series of experiments showed that the silk webbing constitutes an efficient safeguard against dislodgment by waves. When the larvæ are ensconced under these webs, a vigorous dragging and threshing of the leaf through the water in a manner more severe than the effect of a heavy storm in the protected coves, fails in most cases, to wash them away. Possibly, these webs may serve, also, as a partial protection against certain enemies and excessive light, but according to the evidence at hand, its chief rôle is that of an important adaptation to an ever present feature of the aquatic environment.

Peripheral feeding and accompanying silk formation differ in character from the above-described activities. For varying distances the thin edge of the leaf is folded over and tied by strands of silk which extend from the upturned edge to the upper leaf surface. Varying amounts of silk are used in this activity. Instances were observed where the web was thick and brownish, resembling, to some extent, a sort of cocoon. Often, however, it is a fine, thin, dainty webbing through which the larvæ are plainly visible. Feeding invariably occurs under these webs. Peripheral feeding is a very common habit nearly every infested leaf showing evidence of it, and occasional leaves are affected only in this way. Sometimes, the entire margin is turned up and tied over. Funnels formed in this fashion are effective retreats and provide efficiently against the larvæ being washed away by wave-action. Sometimes, the turned over edge collects a small quantity of water, and the larvæ may be partly submerged for a time, although no inconvenience seems to be suffered. Since complete filling of the peripheral tunnels with water is possible, the larvæ may, in such an emergency, escape drowning by migration to the petiole junction—a region more elevated, normally, than the margins and more likely to be free from water. The rare occurrence of pupæ in these upturned margins will be mentioned later. Whether the leaf-feeding period is confined to certain instars was not determined. Exuviæ from small larvæ were frequently seen, particularly under the webbings. Field observations on hundreds of larvæ showed that the surface feeders include individuals up to about 14 mm. in length. It thus appears that more than one instar are included in this period.

Petiole Period.—When a certain growth is attained (apparently about 14 mm.), a distinct change in the feeding habit occurs. Surface feeding under webbings is abandoned and the larva begins to tunnel lengthwise into the upper end of the petiole, boring through from the upper surface. By what means the petiole-leaf junction is located with striking exactness is a matter of conjecture. Instances were observed in which wandering larvæ encountered an uninfested leaf, located immediately the petiole junction and began excavation. Sometimes, the larva bores into one of the chief veins of the leaf, tunneling down it to the petiole. Occasional failure to make exact connection with the end of the petiole, resulting merely in a hole through the leaf, is compensated for by constructing an entrance into the side of the petiole just beneath the leaf. A surface net is often constructed over the petiole-leaf junction beneath which the larva works in forming the burrow. When disturbed, it may leave this shelter, wander about over the leaf for a time, later returning to the web or seeking refuge under old nets at the periphery.

The burrow varies somewhat but usually the length is about 23-70 mm. and the diameter a little greater than that of the larva itself. Its entrance is often surrounded by an accumulation of brownish excrement, the burrow being kept comparatively free from such accumulations. Although most, if not all, of the material excavated from the petiole is passed through the digestive tract of the larva, the principal function of the burrow is other than that of a place to feed since the total length does not exceed double that of the full-grown larva—a condition which would not prevail if it were a true feeding burrow, as in the case of *Bellura melanopyga* (Welch, 1914, p. 102) where burrow length increases with occupancy. Not only is the tunnel always short, but also, once formed, it becomes brown inside, and thereafter shows no evidence of further excavation.

After a burrow long enough to contain the whole larva is constructed, the caterpillar turns about and feeds mostly on the upper surface of the leaf just outside the entrance. Larvæ are frequently observed on the upper leaf surface with only one or two posterior body segments remaining in the burrow. A very slight disturbance, however, causes rapid return. Feeding in this position usually results in elongate surface etchings which radiate from the petiole junction. Sometimes the surface within easy reach from the burrow is completely denuded. It thus appears that the chief function of the burrow is to afford a safe retreat from which surface feeding may be accomplished. This accounts for the fact that an examination of a large number of inhabited petioles showed the head of the larva almost invariably directed towards the leaf. As will appear later, the burrow serves also as a pupation chamber.

At no time was more than one larva found in a burrow, the same being true for the pupæ. Occasionally, a nearly mature individual may, for some unknown reason, desert its burrow and wander about over the *Nelumbo* leaves, ultimately constructing a new burrow in some uninfested leaf or else preëmpting an already formed one which it may chance to find unoccupied. Instances were observed where such a wandering larva attempted to enter a burrow already inhabited, whereupon the occupant and the invader engaged in active combat at the entrance, interlocking mandibles, twisting heads, and pushing each other about in a vigorous manner, until the former succeeded in repulsing the latter, or until the invader forced an entrance, displacing the original occupant.

Effect on Food-plant.—In proportion to the numbers of larvæ present, the leaf of the food-plant loses its chlorophyll-bearing tissue and ultimately shows signs of deterioration. The upper surface shows discoloration, loses its waterproof character, and, in the Sandusky Bay region, usually becomes covered with chironomid (Diptera) larvæ, which form their mud cases all over the exposed surface. Burrow construction partly severs the connection of the leaf with the rootstalk and often results in the ultimate deterioration of the floating part, even in the absence of surface feeding. Since the work of a single larva may lead to leaf deterioration and since it is known that, when present, the buds and seed-capsules are also attacked, it is evident that *P. penitalis* is a serious enemy of *Nelumbo*. The ability of the older larvæ to migrate from leaf to leaf, as described later, also increases their menace to the food-plant.

LOCOMOTION.

Crawling.—Change of position on the food-plant is accomplished by the ordinary methods of crawling. These larvæ are sufficiently active to enable them, where *Nelumbo* leaves are contiguous, to wander widely from the hatching place.

Swimming.—One of the noteworthy adjustments to the aquatic surroundings appears in a well-developed form of surface swimming. Larvæ removed from petiole tunnels and dropped lightly on the water remain supported on the surface. After a few initial squirming movements, active swimming is begun and, as long as nothing interferes with the surface position of the larva, progression is distinctly efficient. Swimming movements consist of an alternate, horizontal, whip-like motion of the posterior half of the body. The sequence of motions is as follows: The posterior end of the body is flexed horizontally on one side into a position in which the caudal end is directed cephalad; then, with a strong, quick sweep, as if released from considerable lateral tension, it returns to the normal position, stopping there for a brief interval; then a similar flexure and return is made on the opposite side. This whip-like motion, first on one side and then on the other, resembles the action of a straight steel spring fixed at one end, bent laterally, suddenly released and stopped at the median position without further vibration; then bent and released on the opposite side. This strong, vigorous return of the posterior end to its normal position constitutes an effective stroke against the water and propels the animal at a goodly rate. So strong is this lateral beat against the water that it swings the anterior end of the larva in the opposite direction, the succeeding stroke swinging it in the reverse direction, thus making the course described by the head a distinct zig-zag, characterized by abrupt rhythmic changes in the lines of progression. While the swimming activities of this larva resemble in many respects, those of the larva of *Bellura melanopyga* (Welch, 1914, pp. 110-112), there is a distinct difference in the swimming movements, since in the latter they are of the graceful sinuous type and lack entirely the jerky character of the former.

As mentioned above, these larvæ swim in a surface depression. They have an integument which resists wetting and enables them to utilize the surface film, but experiments showed that if these caterpillars break entirely through it they sink slowly, performing in vain the swimming movements described above. They seem to have no ability whatever to swim in water and individuals which become completely submerged ultimately go to the bottom. The fate of such larvæ is not known. It is possible that some may return to the surface by crawling up the stems and petioles of floating and emergent vegetation, since experiments showed that they can withstand continued submergence for at least one and one-half hours.

Sometimes a larva gets inverted on the surface film and has great difficulty in righting itself. The swimming activities are continued, however, in the regular way, progress being made until contact with some plant or floating object enables the caterpillar to regain its normal position.

Ordinarily, larvæ seem somewhat unwilling to leave a supporting leaf and take to water, but when sufficiently disturbed they will voluntarily do so. No doubt new retreats and new feeding surfaces are sought in that way also.

RESPIRATION.

Larval Stages.—As mentioned before, the larva has developed no structural adaptations in connection with its aquatic relations. So far as respiration is concerned, it is a typical air-breather and requires direct exposure to the atmosphere. Throughout the whole larval existence, protection against complete submergence is afforded. Certain features of the food-plant aid materially in accomplishing this end. The exposed surface of the leaf is waterproof, due, according to

Pond (1918, p. 181), to many very delicate hairs which enclose an envelope of air, preventing the water from actually touching the epidermis. Unless the leaf has suffered considerable damage, water thrown upon its upper surface rolls off immediately in silvery masses. Some water is occasionally trapped on the surface by upturned margins, but it also fails to wet the surface, and rolls off at the first opportunity. Furthermore, the region of the petiole junction is normally somewhat higher than the surrounding area, thus producing a sloping surface which easily sheds off any water falling upon it. These two features of the plant are effective not only in keeping the exposed surface above water, but in keeping water away from the burrow. Surface feeding ultimately makes the leaf untenable by the removal of the waterproofing provision and the subsequent wetting and submergence of the surface. Except for short accidental periods of submergence, contact of these larvæ with the water is very slight and offers no obstacle to their obligatory holopneustic respiration. Surface swimming also permits dissemination without interference with the usual respiration activities.

All of the burrows which came under the writer's observation seemed remarkably free from water, in spite of the fact that at least a part of each fully constructed burrow is below the water-level outside. In contrast to the larva of *Bellura melanopyga* which lives in a water filled burrow in the petiole of the yellow waterlily and secures oxygen only when at the top, the larva of *P. penitalis* seems to occupy a burrow which is free of standing water and ordinary spiracular respiration is possible at all times.

Pupal Stage.—Although the exact oxygen demands of the pupa are not known, it is fair to assume that they differ but little from other similar pupæ formed in terrestrial environments since the structural features of the respiratory system are the same. Continued submergence of a pupa removed from its silken covering results fatally, indicating that it also must have a certain protection from water. In connection with the field observations, the writer examined many cocoons, none of which contained water. In fact, the pupa appears to be well provided for in this regard. When the full-grown larva begins preparations for pupation, the first activity is the formation of cream-colored, circular, concavo-convex, very closely woven silk cap or plug at the upper end of the tunnel, completely closing it. This plug is quite firm in texture and has a thickness of about 0.7–0.8 mm. over most of its area. At the periphery, where it makes contact with the side of the burrow, it is reduced in thickness to an extremely fine membrane, thus providing for the emergence of the imago. The greater part of the burrow is then lined with a strong, silken cocoon, in the upper end of which the pupa is formed. This cocoon is connected with the above-mentioned cap by means of a vertical curtain of silk. The closing plug and complete cocoon seem to be effective in excluding the water and make it possible for this type of pupa to successfully pass its quiescent period in a position slightly below the water line. That this is an aquatic adaptation is indicated by Chittenden's observation (1918, p. 456), that under the terrestrial conditions of raspberry plants a "small amount of silk is used in the construction of these hibernating chambers, and a little is usually to be found at either end"—a description which in no way applies to the same activities of the larva in the *Nelumbo* petiole. The versatility of this larva in becoming adjusted to different surroundings is manifested by the fact that the writer found a few instances of pupation in the rolled up edges of the *Nelumbo* leaf—instances in which a strong, silken cocoon was formed, but no hint of any special features such as the lid-like cap to the petiole burrow. Nothing can be stated at present concerning the nature of the stimuli or sets of stimuli which are operative in impelling the larva to produce an entirely different cocoon for each of the three known pupation conditions, viz., the petiole burrow, the rolled leaf margin, and the stems of certain terrestrial plants. The fact, however, certainly emphasized the special adjustments which have been developed in connection with the aquatic conditions and which have been superimposed upon a persistent ancestral habit.

While it seems evident that the closing cap at the entrance to the tunnel and the underlying, strong, silken cocoon provide a certain protection against drowning, they are not sufficient to safeguard the pupa from another danger—the larvæ of its own species. It often happens that some larva, wandering on the *Nelumbo* leaves, eats away the closing cap of a pupal chamber, penetrates the upper end of the cocoon, destroys the upper portion of the pupa, and ensconces itself in the re-opened tunnel. Whether the tissues of the pupa were actually used as food or whether the tunnel making instinct of the invading larva caused it to excavate anything which obstructed passage was not determined.

SUMMARY.

1. *Pyrausta penitalis* Grt. (Pyralidæ) occurs abundantly in certain protected situations about Lake Erie in connection with its favorite food plant, *Nelumbo lutea*. It belongs to that extremely limited but interesting, heterogeneous group of Lepidoptera, which has made progress in the development of aquatic adjustments.

2. The life-cycle is imperfectly known. Evidence indicates at least two generations per year. Larvæ and pupæ develop in connection with *Nelumbo*, and eggs, described for the first time, occur on the same plant. Previous writers report relations not only to certain other aquatic plants, but also to two strictly terrestrial ones. Dependable data on the hibernation are lacking.

3. While successfully adjusted to aquatic surroundings, this species has retained the ability to utilize terrestrial conditions, at least to a limited extent. The complete, original, terrestrial organization has apparently been retained also, so that the aquatic adaptations manifested are very largely, if not exclusively, physiological.

4. Surface feeding by young larvæ occurs under silken webs so constructed as to afford adequate protection against dislodgment by wave-action, an ever present menace. The upturned, silk bound margins of the leaf function similarly. Older larvæ construct short petiole tunnels which function only as places for retreat and protection, from which a different type of surface feeding is performed.

5. The older larvæ possess a well-developed, efficient form of surface swimming consisting of an alternate, horizontal, whip-like motion of the posterior portion of the body. They have, however, no ability to swim under the surface and, when completely submerged, sink to the bottom.

6. While an older larva can withstand constant submergence for about one and one-half hours, its typical holopneustic tracheation necessitates access to the atmosphere. Protection from prolonged submergence is provided in part by the water-

proof character of the upper epidermis of the *Nelumbo* leaf and the elevated position of the petiole junction. Surface swimming permits dissemination without serious interference with normal respiration.

7. Pupation occurs in the petiole burrow below the water-level outside and since submergence is fatal, protection is provided not only by the walls of the petiole and the formation of a firm, silken cocoon, but also by the construction of a special closing device—a cream-colored, circular, concavo-convex cap—at the top of the tunnel excluding the water, but providing for the ultimate emergence of the adult. Occasional pupation in the upturned leaf margin is accompanied only by simple cocoon formation, but pupation in terrestrial plants, according to certain writers, appears to be nearly devoid of such provision.

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